ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

May 2003 **Volume 20, N° 3-4**

Alytes, 2003, **20** (3-4) : 93-131.

The *depressor mandibulae* muscle in Anura

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It is well known that the diversity in anuran cranial structure is large, observed in the variation of the bone structure and associated muscles. The *depressor mandibulae* is the jaw muscle that opens the mouth and was considered by many authors useful in delimiting anuran groups. However, there is still much controversy on the value of the m. *depressor mandibulae* as a relationship-indicating character. The goal of this project is to explore the morphological diversity of the *depressor mandibulae* muscle among different families of anurans. Specimens including 60 genera of 17 families of Anura were dissected, using traditional techniques of macroanatomy. Fifteen morphological groups can be distinguished within the anuran species analysed. The insertion point demonstrates little variation. The overall pattern of the origin is also quite stable, except for *Hemisus g. guineensis*, *Arthroleptis* and *Breviceps poweri*, which have an unusual anterior branch of m. *depressor mandibulae* coming from the maxilla. The great diversity in shape of the m. *depressor mandibulae* correlates with the plethora of patterns already mentioned for cranial morphology in Anura. However, it is difficult to assign a specific morphology to a given higher taxon. We also found no evidence that variations in the m. *depressor mandibulae* are associated with particular habits.

INTRODUCTION

In frogs, the *depressor mandibulae* is the jaw muscle that opens the mouth. It is derived from the hyoid arch and innervated by the facial nerve. It has a variable origin and, in general, it occupies the area between the otic branch of the squamosal, the *anulus tympanicus*, and the dorsal fascia.

MUSEUM PARIS

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This muscle is one of the most controversial ones in frogs, evidenced by much discussion around its utility as a phylogenetic character (Griffiths, 1963; Limeses, 1965; Starrett, 1968; Burton, 1983*a-b*, 1986; Lynch, 1993; Burton & Zweifel, 1995; La Marca, 1995; Manzano, 1996, 1997; Hoyos, 1999). Many of these authors (Burton, 1983*a-b*; Myers & Ford, 1986; Ford, 1989; Savage, 1987; Ford & Cannatella, 1993) considered that the m. *depressor mandibulae* is useful to delimit anuran groups. Nevertheless, other authors affirmed that the morphology of the m. *depressor mandibulae* does not form consistent patterns with cladistic or phenetic hypotheses (Lynch, 1993; Hoyos, 1999).

Reviewing pseudid and hylid myology it was found (AM) that the m. *depressor mandibulae* presents a distinctive morphology in pseudids and phyllomedusine frogs. The amount of contradictory discussion led us to undertake a morphological descriptive survey of the m. *depressor mandibulae* among anurans. The goal of this project is to explore the morphological diversity of *depressor mandibulae* muscle among sixteen families of Anura.

MATERIALS AND METHODS

Two hundred and twenty seven specimens belonging to seventeen families of Anura (60 genera) were dissected under a stereomicroscope (app. 1). The skin was removed from the cervical and cranial regions (both sides) on each specimen, exposing the *depressor mandibulae* and adjacent musculature. When the muscle was divided, we removed the layers from the most superficial to the deepest. Each dissection was described in detail, focusing especially on the sites of origin and insertion, general morphological characteristics, and the relation of the m. *depressor mandibulae* with other structures (bones, blood vessels, nerves and other muscles). In some cases (particularly in small animals), differential staining with iodine solution (Bock & Shear, 1972) was done. Bones and cartilages of some specimens were stained with alizarine red S and Alcian blue 8GX, respectively, as described by Wassersug (1976). The terminology used for bone follows Trueb (1993) and muscle terminology follows Duellman & Trueb (1985). All the material is deposited in the herpetological collection of the Fundación Miguel Lillo (FML), the herpetological collection of the Centro de Investigaciones y Transferencia de Tecnologia a la Producción (DIAM), Universidad del Valle de Cali (Colombia) (UVC) and the African collection of Dr. Raymond Laurent (RL).

We consider that there are three generalized origin points of the *depressor mandibulae* muscle: *anulus tympanicus*, squamosal and/or dorsal facia. When the muscle is divided in two branches, we define the anterior branch as that branch corresponding to the first branch present in a cephalo-caudal axis. When the anterior branch is overlapped by a branch, we define this condition as deep anterior branch, and superficial anterior branch respectively. The posterior one is that branch present behind the anterior branch. When an extra branch is ahead of our anterior branch, we define that using a name related with its origin point. When the muscle is divided in an external branch and an internal branch, we define those as superficial *depressor mandibulae* and deep *depressor mandibulae* respectively.

To improve our understanding we gathered in groups, species that share similar conditions of *depressor mandibulae* muscle in a table (tab. 1), adding schematic drawings – with special reference to the origin points and general morphology, since the insertion points are stable –, and used Starrett's (1968) nomenclature with our modifications. Starrett (1968) proposed a notation system for the different *depressor mandibulae* morphologies. We used this notation for our patterns (tab. 1) but found that it was necessary to define new states that were not considered by the Starrett system. For example, the morphology of *Hemisus guineensis guineensis* needs new letters (mx) to describe the branch's origin on the maxilla. Where amuscle division into branches is present, it is represented by a dash. There is a limitation of this nomenclature to describe different branch shapes. For example, the same notation is used to symbolize our groups XIIb and XIIc, despite having differences between them. For that reason we used the subindex 1 and 2 respectively.

RESULTS

FAMILY DISCOGLOSSIDAE

Alytes obstetricans (fig. 1a). – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia (on the upper part of the m. *dorsalis scapulae*) and m. *levator mandibulae posterioris longus*. The m. *depressor mandibulae* is elongated and approximately triangular, and inserts on the articular process of the lower jaw.

FAMILY PIPIDAE

Hymenochirus boettgeri camerunensis. – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal and posterior edge of the *anulus tympanicus*. It is approximately rectangular, short, bulky and wider at the origin. The m. *depressor mandibulae* does not contact the m. *dorsalis scapulae*. It inserts on the articular process of the lower jaw.

Xenopus laevis. – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia at the level of the inferior edge of m. *levator mandibulae posterioris longus*, superior edge of the dorsal branch of m. *dorsalis scapulae*, and lateral edge of the m. *romboideus anterior*. The m. *depressor mandibulae* is elongated and approximately triangular, and inserts on the articular process of lower jaw.

FAMILY BUFONIDAE

Bufo arenarum. – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal. It is bulky and approximately fusiform, wider at the origin and is quite apart from the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Bufo granulosus major. – It has a single *depressor mandibulae* muscle, but with fibers partially dividing at the origin, arranged bundle-like in different directions, imbricating with each other. It is fusiform and narrow, and covers the m. *cucularis* (= *sternocleidomastoideus*). It originates from the posterior edge of the *anulus tympanicus* and posterior end of the otic process of the squamosal. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Bufo paracnemis. – It has a single *depressor mandibulae* muscle that originates from the otic branch of the squamosal. It is an approximately rectangular and slightly bulky muscle, wider

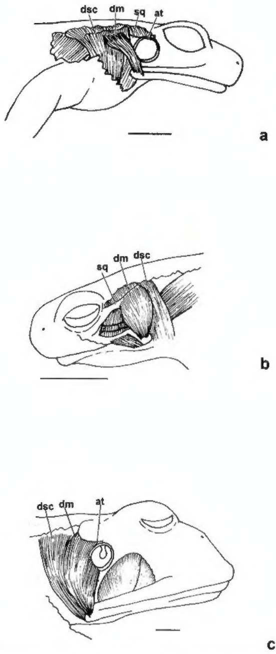

Fig. 1. – (a) *Alytes obstetricans* (FML 02782). Morphology corresponding to group I (tab. 1). Scale bar: 0.5 mm. – (b) *Melanophryniscus rubriventris rubriventris* (FML 02502). Morphology corresponding to group IIb (tab. 1). Scale bar: 0.5 mm. – (c) *Ceratophrys cranwelli* (FML 04924). Morphology corresponding to group IIc (tab. 1). Scale bar: 0.5 mm. – Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dsc, m. *dorsalis scapulae*; sq, squamosal.

at the origin and does not cover the m. *dorsalis scapulae*. It inserts on the articular process of the lower law.

Bufo spinulosus. – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal. It is bulky and fusiform, and is formed by bundles of fibers that split easily. It partially covers the m. *cucularis*. The m. *depressor mandibulae* inserts on the articular process of the lower law.

Melanophryniscus rubriventris rubriventris (fig. 1b). – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal. It is a fan-shaped and bulky muscle, wide at the origin (the last characteristic only in some specimens) and does not contact the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

FAMILY LEPTODACTYLIDAE

Ceratophryinae

Ceratophrys cranwelli (fig 1c). – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal, covered by the *osiculum*, on the posterior border of the *anulus tympanicus* and dorsal fascia (at the level of the m. *dorsalis scapulae*). It is an irregular and thick muscle, wide at the origin and narrow at the insertion. It partially covers the m. *dorsalis scapulae* and inserts on the articular process of the lower jaw.

Chacophrys pierotti (fig. 2a). – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal, the posterior border of the *anulus tympanicus* and dorsal fascia (at the level of the m. *dorsalis scapulae*). It is an irregular muscle, wide at the origin and narrow at the insertion. It partially covers the m. *dorsalis scapulae* and inserts on the articular process of the lower jaw.

Lepidobatrachus llanensis (fig. 2b). – It has a single *depressor mandibulae* muscle, fusiform, very thick and long. It originates on the posterior edge of the *anulus tympanicus* and otic process of the squamosal, and inserts on the articular process of the lower jaw.

Hylodinae

Crossodactylus gaudichaudii (fig. 2c). – It has a thin, short, and fan-shaped *depressor mandibulae* muscle divided into two branches joined at mid-muscle level. Anterior fibers originate on the otic process of the squamosal, and the posterior fibers originate from the dorsal fascia (at the level of the posteromesial edge of the m. *dorsalis scapulae*). The posterior branch is longer than the anterior. It inserts on the articular process of the lower jaw by a short tendon.

Leptodactylinae

Leptodactylus bufonius (fig. 3a). – It has a wide and approximately triangular *depressor mandibulae* muscle divided into two branches joined at mid-muscle level. The anterior fibers originate from the otic process of the squamosal and posterior fibers from the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae* and m. *latissimus dorsi*). The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Leptodactylus chaquensis (fig. 3b). – It has a single *depressor mandibulae* muscle with a subtle division at its origin. It originates on the otic process of the squamosal and dorsal fascia (at

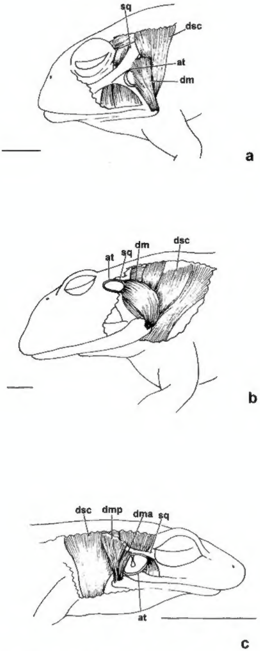

Fig. 2. – (a) *Chacophrys pierotti* (FML 01020). Morphology corresponding to group IIa (tab. 1). Scale bar: 0.5 mm. – (b) *Lepidobatrachus llanensis* (FML 01095). Morphology corresponding to group IIc (tab. 1). Scale bar: 0.5 mm. – (c) *Crossodactylus gaudichaudii* (FML 03497). Morphology corresponding to group III (tab. 1). Scale bar: 0.5 mm. – Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

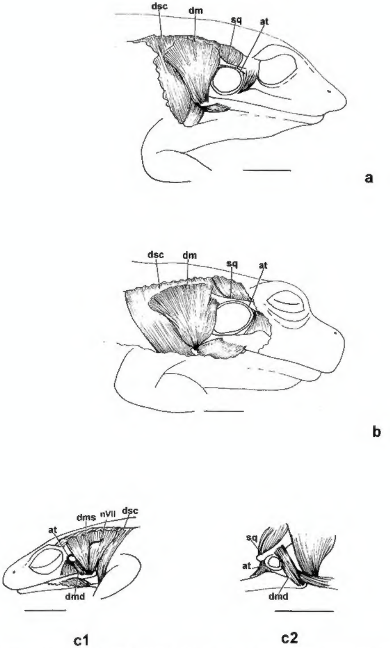

Fig. 3. – (a) *Leptodactylus bufonius* (FML 04642). Morphology corresponding to group III (tab. 1). Scale bar: 0.5 mm. – (b) *Leptodactylus chaquensis* (FML 05490). Morphology corresponding to group III (tab. 1). Scale bar: 0.5 mm. – (c1) *Pseudopaludicola boliviana* (FML 04307). Morphology corresponding to group Vc (tab. 1). Scale bar: 0.2 mm. – (c2) Detail of deep m. *depressor mandibulae* of *P. boliviana*. Scale bar: 0.2 mm. – Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dmd, deep m. *depressor mandibulae*; dms, superficial m. *depressor mandibulae*; dsc, m. *dorsalis scapulae*; nVII, branch of the nerve VII; sq, squamosal.

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the level of mesial edge of the m. *dorsalis scapulae* and m. *latissimus dorsi*). The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Pleurodema borellii. – It has a *depressor mandibulae* muscle divided into two slips, the anterior branch originates from the otic process of the squamosal. It is approximately triangular, wide at the origin. The posterior branch originates from the dorsal fascia (at the level of mesial edge of the m. *dorsalis scapulae* and m. *latissimus dorsi*). It is thicker and wider that the anterior branch. Both branches insert on the articular process of the lower jaw.

Physalaemus biligonigerus. – It has a *depressor mandibulae* muscle divided into two branches joined at mid-muscle level. The anterior branch is short and triangular and originates from the otic process of the squamosal. The posterior branch is triangular and wide and originates from the dorsal fascia (at the level of the middle region of the m. *dorsalis scapulae*). Both branches are inserted on the articular process of the lower jaw.

Pseudopaludicola boliviana (fig. 3c). – It has a *depressor mandibulae* muscle divided into two slips. A large and fan-shaped superficial slip arises from the dorsal fascia (at the level of the cervical muscles, partially covering the m. *levator scapulae*). This slip is very wide and thin at the origin, and it extends extensively on the dorsal region of the trunk. It covers the posterior part of the *anulus tympanicus* without adhering to it. A nerve V branch passes through the superficial slip. An approximately rectangular, flat and small deep slip originates on the otic process of the squamosal (with some anterior fibers contacting the posterior edge of the *anulus tympanicus*). It contacts the m. *cucularis* at the origin, partially covering it. Both branches of the m. *depressor mandibulae* insert on the articular process of the lower jaw.

Telmatobiinae

Alsodes sp. – It has a *depressor mandibulae* muscle divided into two slips. A thick and rectangular anterior slip originates from the otic process of the squamosal, and a posterior slip that originates from the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*). The posterior slip is longer than the anterior. Both branches insert on the posterior end of the articular process of the lower jaw.

Batrachyla sp. – It has a *depressor mandibulae* muscle divided into two slips. An approximately rectangular, short, and thick anterior slip originates from the otic process of the squamosal. The posterior slip, approximately triangular, long, and thin, originates from the dorsal fascia (at the level of the middle region of the m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

Hylorina sylvatica. – It has a *depressor mandibulae* muscle divided into two equally long slips. The anterior slip is thick and rectangular and arises from the otic process of the squamosal. The posterior one, triangular and thicker than the anterior, originates from the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

Telmatobius laticeps (fig. 4a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip is approximately rectangular, narrow, and thick. It originates on the otic process of the squamosal. The posterior slip, approximately triangular and wide at the origin, arises from the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

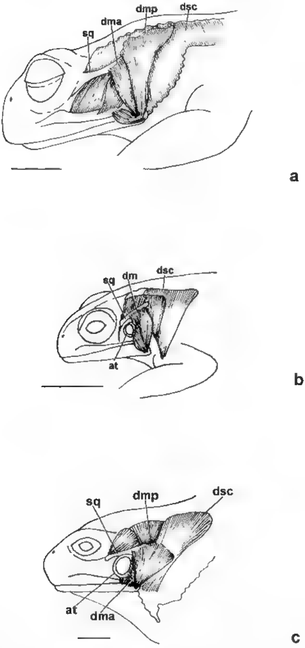


Fig. 4. — (a) *Telmatobius laticeps* (FML 03960). Morphology corresponding to group X (tab. 1). Sacle bar 0.5 mm. — (b) *Crinia georgiana* (DIAM 015). Morphology corresponding to group IIc (tab. 1). Scale bar 0.5 mm. — (c) *Limnodynastes fletcheri* (DIAM 009). Morphology corresponding to group Va (tab. 1). Scale bar 0.5 mm. Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

Telmatobius scrocchii. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip is approximately triangular, narrow, short and thick. It arises from the otic process of the squamosal. The posterior slip originates from the dorsal fascia (at the level of the middle region of the m. *dorsalis scapulae* and the most anterior fibers at the level of the otoccipital). It is triangular, longer, and twice as thick as the anterior slip. Both branches insert on the articular process of the lower jaw.

Telmatobius oxycephalus. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular and narrow, originates from the otic process of the squamosal. The posterior slip, triangular, wide, and longer than the anterior, originates from the dorsal fascia (at the level of the middle region of the m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

FAMILY MYOBATRACHIDAE

Myobatrachinae

Crinia georgiana (fig. 4b). – It has a bulky and fusiform single *depressor mandibulae* muscle. It arises from the otic process of the squamosal and the posterior edge of the *anulus tympanicus*, partially covering it. The m. *depressor mandibulae* does not cover the m. *dorsalis scapulae*. There are two kinds of fibers, anterior fibers parallel to the posterior edge of the *anulus tympanicus*, and posterior fibers oriented perpendicular to anterior ones. The m. *depressor mandibulae* inserts on the posterior edge of the lower jaw by a tendon.

Taudactylus diurnus. – It has a fan-shaped single *depressor mandibulae* muscle, wide at its origin. Some anterior fibers originate from the otic process of the squamosal. Posterior fibers arise from the dorsal fascia (at the level of the anteromesial edge of m. *dorsalis scapulae*). The m. *depressor mandibulae* inserts on the articular process of the lower jaw by a short and thick tendon.

Uperoleia aspera. – It has a long and bulky single *depressor mandibulae* muscle, partially covering the tympanum. It originates on the dorsal fascia (at the level of the occipital and otic process of the squamosal); the anterior fibers are partially divided originating on the posterodorsal edge of the *anulus tympanicus*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw by a short tendon.

Uperoleia borealis. – It has a *depressor mandibulae* muscle divided into two slips. An anterior slip originates on the posterior edge of the *anulus tympanicus*. This slip is flat and approximately rectangular, and is partially covered by the posterior slip. The posterior slip originates on the external surface of the otic process of the squamosal and the dorsal fascia. It is approximately triangular, wider at the origin and does not contact the m. *dorsalis scapulae*. Both branches insert on the articular process of the lower jaw.

Limnodynastinae

Limnodynastes dumerili. – It has a *depressor mandibulae* muscle divided into two slips. An anterior and approximately rectangular slip originates on the ventral edge of the *anulus tympanicus* and otic process of the squamosal, partially covered by the posterior branch. The posterior slip originates on the dorsal fascia, partially covering the m. *dorsalis scapulae*. It is wide and approximately triangular, slightly curved at the origin, surrounding the middle anterior edge of m. *dorsalis scapulae* Both branches insert on the articular process of the lower jaw.

Limnodynastes convexiusculus It has a *depressor mandibulae* muscle divided into two slips. An anterior slip originates on the posteroventral edge of the *anulus tympanicus*. It is approximately quadrangular, very short, thin, and narrow. The posterior slip is narrow, elongated and has a noticeable curve caudad. It originates on the dorsal fascia (at the level of the anterior edge of the suprascapula, partially covering the m. *dorsalis scapulae*) Both branches insert on the articular process of the lower jaw.

Limnodynastes dorsalis It has a *depressor mandibulae* muscle divided into two slips. An anterior slip, very thin and short, originates on the posterior edge of the *anulus tympanicus*. The posterior slip is fan-shaped and very wide that originates from the dorsal fascia (at the level of the medial edge of m. *dorsalis scapulae* and the otic process of the squamosal). It partially covers the anterior branch. Both branches insert on the articular process of the lower jaw by a tendon.

Limnodynastes fletcheri (fig. 4c) It has a *depressor mandibulae* muscle divided into two slips. An anterior approximately triangular, very thin, and short slip originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae*) and the otic process of the squamosal It is fan-shaped and wide at the origin, and partially covers the anterior branch Both branches insert on the articular process of the lower jaw.

Limnodynastes ornatus. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular and very short, originates on the posterior edge of the *anulus tympanicus*. The posterior slip is fan-shaped and wide at the origin and originates from the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae* and the otic process of the squamosal). It partially covers the anterior branch. Both branches insert on the articular process of the lower jaw.

Notaden melanoscaphus (fig. 5a) It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular, long and narrow, originates from the otic process of the squamosal The posterior slip originates on the dorsal fascia (at the level of the origin of the m *dorsalis scapulae*) It is approximately rectangular and longer than the anterior slip and is very narrow and curved, crossing over middle part of the m *cucullaris* Both branches insert on the articular process of the lower jaw.

Notaden nichollsi. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately fusiform and long, originates on the otic process of the squamosal. The posterior slip originates on the dorsal fascia (at the level of the origin of the m. *dorsalis scapulae*). It is approximately rectangular and longer than the anterior slip, very narrow and curved. Both branches insert on the articular process of the lower jaw.

FAMILY RHINODERMATIDAE

Rhinoderma darwinii (fig 5b) It has a single *depressor mandibulae* muscle, approximately triangular and wide at the origin It contacts the anterior border of the m *dorsalis scapulae*

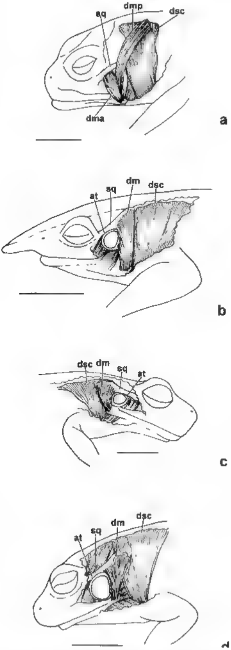


Fig. 5. (a) *Notaden melanoscaphus* (FML 03783). Morphology corresponding to group IX (tab. 1). Scale bar: 0.5 mm. (b) *Rhinoderma darwinii* (FML 03694). Morphology corresponding to group VIIa (tab. 1). Scale bar: 0.5 mm. (c) *Gastrotheca christiani* (FML 02117). Morphology corresponding to group IV (tab. 1). Scale bar: 0.5 mm. (d) *Gastrotheca gracilis* (FML 01769). Morphology corresponding to group IV (tab. 1). Scale bar: 0.5 mm. Abbreviations: at, *annulus tympanicus*; dm, m. *depressor mandibulae*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

It has anterior fibers originating on the posterior edge of the *anulus tympanicus*. The posterior fibers originate from the posterior end of the otic process of the squamosal. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

FAMILY HYLIDAE

Hemiphractinae

Gastrotheca christiani (fig. 5c). – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia, the otic process of the squamosal, and the posterior edge of the *anulus tympanicus*. Approximately rectangular and wide at the origin, it contacts with the anterior border of the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Gastrotheca chrysosticta. – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia, the otic process of the squamosal, and the posterior edge of the *anulus tympanicus*. Approximately rectangular, wide at the origin, it contacts the anterior border of the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Gastrotheca gracilis (fig. 5d). – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia, the otic process of the squamosal, and the posterior edge of the *anulus tympanicus*. Approximately triangular and wide at the origin, the muscle contacts the anterior border of the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Hylinae

Acris crepitans (fig. 6a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular and elongated, originates on the otic process of the squamosal, and partially covers the posterior edge of the *anulus tympanicus*. The posterior slip, very narrow, thin, and curved, originates on the dorsal fascia (at the level of the middle part of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

Argenteohyla siemersi. – It has a *depressor mandibulae* muscle divided into three slips. The anterior slip, approximately rectangular and narrow, originates on the posterior edge of the *anulus tympanicus*. The middle slip, approximately rectangular and wide at the origin (longer than anterior slip), originates on the posterior edge of otic process of the squamosal. The posterior slip, triangular and wide (longer than middle slip), originates on the dorsal fascia (at the level of the middle part of m. *dorsalis scapulae*). The three branches insert on the articular process of the lower jaw.

Hyla boans (fig. 6b). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular (wider at the origin) originates on the posterior edge of the otic process of the squamosal. The posterior slip, approximately triangular and wide at the origin (longer than anterior slip), originates on the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

Hyla andina. – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal and the posterior edge of the *anulus tympanicus*. It is approximately

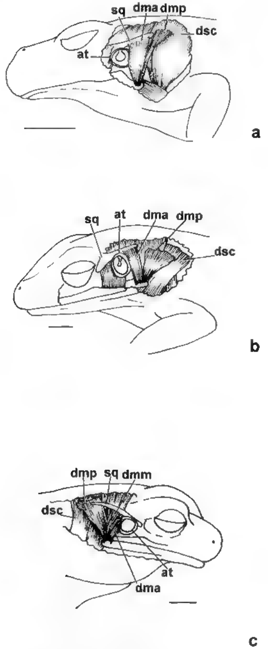


Fig. 6. – (a) *Acris crepitans* (RL 017838). Morphology corresponding to group IX (tab. 1). Scale bar 0.3 mm. (b) *Hyla boans* (FML 09543). Morphology corresponding to group X (tab. 1). Scale bar 0.5. (c) *Phrynohyas venulosa* (FML 02303). Morphology corresponding to group XI (tab. 1). Scale bar 0.5 mm. Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmm, m. *depressor mandibulae medialis*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

triangular, wider at the origin and does not contact with m. *dorsalis scapulae* The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Phrynohyas venulosa (fig. 6c) It has a *depressor mandibulae* muscle divided into three slips. The anterior slip is short and approximately rectangular and originates on the ventral edge of the *anulus tympanicus* The middle slip is wide and partially covered by the anterior slip (the otic process of the squamosal crossing over it) It originates on the epimysium of the lateral edge of m. *levator mandibulae posterioris longus*. The posterior slip, long and approximately triangular, arises from the dorsal fascia (at the level of the suprascapula) and contacts the m *levator scapulae*. The three branches insert on the articular process of the lower jaw by a thick, wide and very short tendon.

Plectrohyla guatemalensis. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip arises from the otic process of the squamosal. It is very thin, approximately rectangular, and short. The posterior slip originates from the dorsal fascia (at the level of the mesial edge of the suprascapula). It is very wide and approximately triangular. Both branches insert on the articular process of the lower jaw.

Ptychohyla ignicolor It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates from the otic process of the squamosal. It is thick and approximately rectangular. The posterior slip originates from the dorsal fascia (at the level of the edge of the anterior half of the m *dorsalis scapulae*). It is very thin and approximately rectangular. Both branches insert on the articular process of the lower jaw by a short tendon

Scinax fuscovarius (fig 7a) It has a fan-shaped single *depressor mandibulae* muscle (wide at the origin) that originates from the dorsal fascia (at the level of the superior branch of m. *dorsalis scapulae*), otic process of the squamosal, and the anterior fibers on the posterior edge of *anulus tympanicus*. It inserts on the articular process of the lower jaw.

Smilisca sila It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates from the posterior end of the otic process of the squamosal. It is long, narrow, and approximately rectangular The posterior slip originates from the dorsal fascia (at the level of the mesial half of the m. *dorsalis scapulae*). It is long, thin, approximately rectangular, and curved. Both branches insert on the articular process of the lower jaw

Phyllomedusinae

Agalychnis saltator (fig 7b). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip arises from the posteroventral edge of the *anulus tympanicus*. It is approximately rectangular, short, and thin The posterior slip arises from the otic process of the squamosal. It is very thick, wide, and approximately rectangular. Both branches insert on the articular process of the lower jaw

Phyllomedusa boliviana It has a *depressor mandibulae* muscle divided into three slips. The anterior slip originates from the posteroventral edge of the *anulus tympanicus* It is approximately rectangular, short, and thin The middle slip is approximately triangular (wider at the origin). It arises from the otic process of the squamosal, and partially covers the posterior slip, which arises from the dorsal fascia (at the level of the anterior edge of the m *dorsalis scapulae*) It is long, curved, and approximately triangular, it covers the anterior edge of the m *dorsalis scapulae* The three branches insert on the articular process of the lower jaw

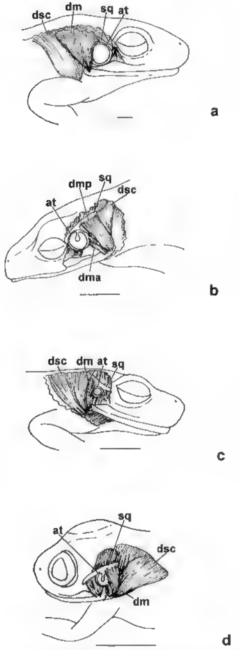


Fig. 7. (a) *Scinax fuscovarius* (FML 04635). Morphology corresponding to group IV (tab. 1). Scale bar 0.5 mm. (b) *Agalychnis saltator* (FML 09541). Morphology corresponding to group VIIb (tab. 1). Scale bar: 0.5 mm. (c) *Centrolene grandisonae* (FML 04980). Morphology corresponding to group VIIa (tab. 1). Scale bar: 0.5 mm. (d) *Cochranella ignota* (UVC 12091). Morphology corresponding to group VIIa (tab. 1). Scale bar: 0.5 mm. Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

Phyllomedusa hypocondrialis. – It has a *depressor mandibulae* muscle divided into three slips. The anterior slip originates from the ventral edge of the *anulus tympanicus* It is approximately rectangular, short, and thin The middle slip originates from the otic process of the squamosal. It is approximately rectangular, wide at the origin. The posterior slip originates from the dorsal fascia (at the level of the anterior edge of m. *dorsalis scapulae*) It is long, thin, approximately triangular, and curved. It covers the anterior edge of m. *dorsalis scapulae*. The three branches insert on the articular process of the lower jaw.

Phyllomedusa sauvagii It has a *depressor mandibulae* muscle divided into three slips. The anterior slip originates from the posteroventral edge of *anulus tympanicus*. It is approximately rectangular and thin. The middle slip originates from the otic process of the squamosal. It is approximately triangular (wide at the origin)and partially covers the posterior slip. The posterior slip originates from the dorsal fascia (at the level of the middle region of the m *dorsalis scapulae*) It is long and approximately rectangular. It covers the anterior half of the m. *dorsalis scapulae* The three branches insert on the articular process of the lower jaw

FAMILY CENTROLENIDAE

Centrolene grandisonae (fig 7c). It has a single *depressor mandibulae* muscle. It originates on the posterior edge of the *anulus tympanicus* and the otic process of the squamosal It is short, small and approximately triangular It does not contact the m. *dorsalis scapulae* The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

Cochranella ignota (fig. 7d). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip arises from the posteroventral edge of the *anulus tympanicus*. It is approximately rectangular, short, and thin The posterior slip is approximately triangular and it originates on the otic process of the squamosal. It does not contact the m. *dorsalis scapulae*. It inserts on the articular process of the lower jaw.

FAMILY PSEUDIDAE

Lysapsus limellus (fig. 8a) It has a single *depressor mandibulae* muscle. It originates on the posterior edge of the *anulus tympanicus*, the otic process of the squamosal, and the dorsal fascia. The m. *depressor mandibulae* is approximately triangular, wider at the origin, and contacts the m *dorsalis scapulae* The m *depressor mandibulae* inserts on the articular process of the lower jaw.

Pseudis minutus (fig 8b) It has a single *depressor mandibulae* muscle that originates on the posterior edge of the *anulus tympanicus*, the otic process of the squamosal, and the dorsal fascia It is a very thick, wide and fan-shaped muscle that contacts the m. *dorsalis scapulae* The m *depressor mandibulae* inserts on the articular process of the lower jaw

Pseudis paradoxus (fig 8c). – It has a single *depressor mandibulae* muscle. It originates on the posterior edge of the *anulus tympanicus*, the otic process of the squamosal, and the dorsal fascia. It is a long, fan-shaped muscle, which contacts the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw

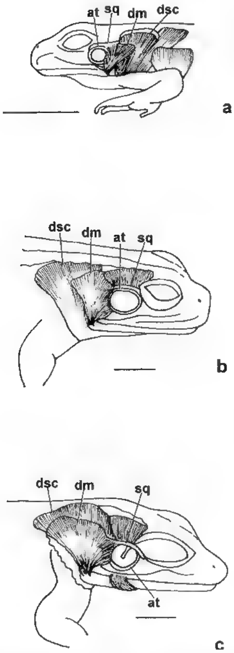


Fig. 8. — (a) *Lysapsus limellus* (FML 00791). Morphology corresponding to group IV (tab. 1). Scale bar: 0.5 mm. — (b) *Pseudis minutus* (FML 03676). Morphology corresponding to group IV (tab. 1). Scale bar: 0.5 mm. — (c) *Pseudis paradoxus* (FML 00936). Morphology corresponding to group IV (tab. 1). Scale bar: 0.5 mm. — Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dsc, m. *dorsalis scapulae*; sq, squamosal.

FAMILY MICROHYLIDAE

Brevicipitinae

Breviceps poweri (fig 9a). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the posterior end of the maxilla by a short tendon. It is thick, short, and approximately fusiform. The posterior slip originates on the otic process of the squamosal This slip is long, thick, and approximately triangular Both branches insert on the articular process of the lower jaw.

Microhylinae

Dermatonotus muelleri (fig 9b). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the ventral edge of the *anulus tympanicus* It is short, thick, and approximately rectangular The posterior slip originates from the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae* and the m. *latissimus dorsi*, almost reaching the posterior edge of the eyes). It is long, thick, approximately triangular, and very wide at the origin. Both branches insert on the articular process of the lower jaw.

Elachistocleis bicolor (fig. 9c). - It has a single *depressor mandibulae* muscle It originates from the ventral and anterior edge of the *anulus tympanicus* and the dorsal fascia (at the level of the anterior edge of the m. *dorsalis scapulae* and the m. *latissimus dorsi*). The m *depressor mandibulae* is a very wide and fan-shaped muscle that partially covers the tympanum, the jugal and the posterior edge of the maxilla. A branch of cranial nerve VII passes through it. The muscle inserts on the articular process of the lower jaw

Phrynomerinae

Phrynomantis bifasciatus. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the lateral edge of the *anulus tympanicus*. It is short, thick, and approximately rectangular The posterior slip originates on the dorsal fascia, and covers the mesial edge of the m *cucullaris* and the anteromedial edge of the m *dorsalis scapulae* It is a fan-shaped muscle with a longer posterodorsal projection It surrounds the posterior edge of the tympanum A branch of cranial nerve VII passes through it. Both branches insert on the articular process of the lower jaw.

FAMILY DENDROBATIDAE

Colostethus subpunctatus It has a *depressor mandibulae* muscle divided into two slips. The superficial slip originates from the dorsal fascia (at the level of the m. *dorsalis scapulae* and the m. *levator mandibulae posterioris longus*). It is a wide and fan-shaped muscle The deep slip originates on the posterior edge of the *anulus tympanicus* and the otic process of the squamosal It is short, small, and rectangular Both branches insert on the articular process of the lower jaw.

Dendrobates auratus (fig. 10a). It has a *depressor mandibulae* muscle partially divided into three slips. The anterior slip originates from the dorsal fascia (at the level of the m *dorsalis scapulae* and the m. *levator mandibulae posterioris longus*). It is approximately triangular and

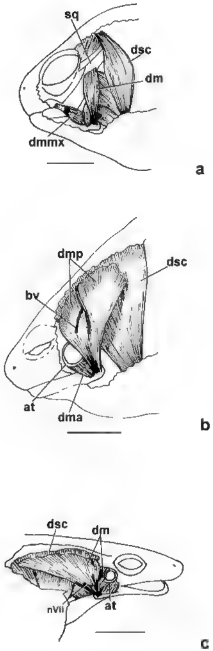


Fig. 9. – (a) *Breviceps poweri* (FML 03165). Morphology corresponding to group VIc (tab. 1). Scale bar: 0.5 mm. (b) *Dermatonotus muelleri* (FML 05365). Morphology corresponding to group XIIb (tab. 1). Scale bar: 0.5 mm. (c) *Elachistocleis bicolor* (FML 00251). Morphology corresponding to group XIIa (tab. 1). Scale bar: 0.5 mm. Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmmx, m. *depressor mandibulae maxillaris*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; bv, branch of the nerve VII; sq, squamosal.

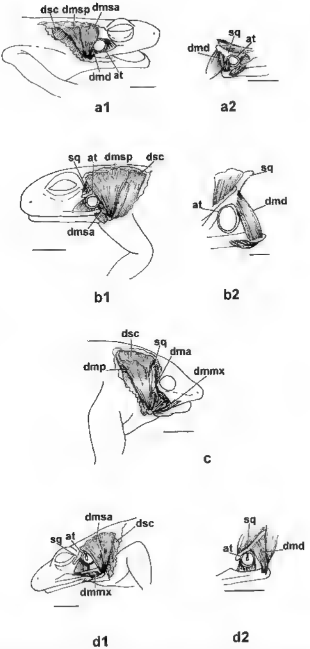


Fig. 10 (a1) *Dendrobates auratus* (FML 01722) Morphology corresponding to group Vb (tab. 1). Scale bar 0.5 mm (a2) Detail of deep m *depressor mandibulae* of *D. auratus*. Scale bar 0.5 mm – (b1) *Epipedobates pictus* (FML 03516). Morphology corresponding to group Vd (tab. 1) Scale bar: 0.3 mm (b2) Detail of deep m. *depressor mandibulae* of *E. pictus*. Scale bar: 0.1 mm – (c) *Hemisus guineensis guineensis* (FML 01244) Morphology corresponding to group VIa (tab. 1) Scale bar 0.5 mm (d1) *Arthroleptus tuberosus* (FML 00051) Morphology corresponding to group VIb (tab. 1) Scale bar 0.3 mm (d2) Detail of deep m *depressor mandibulae* of *A. tuberosus* Scale bar 0.3 mm Abbreviations at, *anulus tympanicus*, dma, m *depressor mandibulae anterior*, dmd, deep m *depressor mandibulae*, dmmx, m. *depressor mandibule maxilaris*, dmp, m *depressor mandibulae posterior*; dmsa, m *depressor mandibulae superficial anterior*, dmsp, m *depressor mandibulae superficial posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal

wider at the origin. The posterior slip originates from the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is approximately rectangular and as long as the anterior slip. A deep slip originates on the posterior edge of the *anulus tympanicus* and the otic process of the squamosal. It is short, approximately rectangular, wide at the origin. The three branches insert on the articular process of the lower jaw.

Epipedobates pictus (fig. 10b) – It has a *depressor mandibulae* muscle divided into two slips; the superficial one is partially divided. The anterior superficial slip, which is short and rectangular, originates on the posterior edge of the *anulus tympanicus*. The posterior superficial slip originates from the dorsal fascia (at the level of the posterolateral region of the anteromesial part of the m. *dorsalis scapulae*). A deep slip, narrow and rectangular, originates on the otic process of the squamosal and the posteroventral edge of the *anulus tympanicus*. The three branches insert on the articular process of the lower jaw, the deep slip mesial to superficial slips.

FAMILY HEMISOTIDAE

Hemisus guineensis guineensis (fig. 10c) – It has a *depressor mandibulae* muscle divided into three slips. The anterior slip, short and fusiform, originates on the alary process of the maxilla by a tendon. The middle rectangular slip originates on the otic process of the squamosal. The posterior slip originates on the dorsal fascia (at the level of the suprascapula, partially covering the m. *dorsalis scapulae* and the m. *latissimus dorsi*). It is triangular and broad, curving toward the posterior region of the body. The three branches insert on the posterior end of the quadrate.

FAMILY ARTHROLEPTIDAE

Arthroleptinae

Arthroleptis tuberosus (fig. 10d) – It has a *depressor mandibulae* muscle divided into three slips. The anterior superficial slip originates on the posterior edge of the maxilla. It is long, very thin, and approximately fusiform. The posterior superficial slip is fan-shaped and wide at its origin on the dorsal fascia. It partially covers the m. *dorsalis scapulae* and m. *latissimus dorsi*, and completely covers the deep slip. The deep slip, approximately rectangular and slightly wider at its origin, originates on the otic process of the squamosal. It partially covers the posterior border of the tympanum. The three branches insert on the articular process of the lower jaw.

Arthroleptis stenodactylus stenodactylus – It has a *depressor mandibulae* muscle divided into three slips. The anterior superficial slip originates on the posterior edge of the maxilla. It is long, very thin, and approximately fusiform. The posterior superficial slip, fan-shaped and wide at its origin on the dorsal fascia, covers the m. *dorsalis scapulae* and m. *latissimus dorsi*. The deep slip, approximately rectangular, originates on the otic process of the squamosal. It partially covers the posterior border of the tympanum. The three branches insert on the articular process of the lower jaw.

Schoutedenella sp. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and rectangular, is wide at the origin and originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip, fan-shaped and wider at the origin, originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). Its posterior part partially covers the suprascapula. Both branches insert on the articular process of the lower jaw.

Schoutedenella sylvatica. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and rectangular, is wide at the origin and originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is fan-shaped and wider at the origin with a posterior part that partially covers the suprascapula. Both branches insert on the articular process of the lower jaw.

Cardioglossa sp. (fig. 11a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip is short, rectangular, and thick, originating from the otic branch of the squamosal at the posteroventral edge of the *anulus tympanicus*. The posterior slip is fan-shaped and wider at the origin, originating on the dorsal fascia (at the level of the m. *dorsalis scapulae* and the m. *rhomboideus* anterior). A nerve V branch passes through its fibers at mid-level. This slip partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

FAMILY RANIDAE

Dicroglossinae

Conraua crassipes. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the inferior edge of the *anulus tympanicus*. The posterior fan-shaped slip, wider at the origin, originates on the dorsal fascia (at the level of the dorsal part of the m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw by a short tendon.

Hoplobatrachus occipitalis. – It has a single *depressor mandibulae* muscle. It originates on the inferior edge of the *anulus tympanicus* and the dorsal fascia (at the level of the anterodorsal part of the m. *dorsalis scapulae*, covering most of it). The *depressor mandibulae* is a fan-shaped and very wide muscle. It inserts on the articular process of the lower jaw by a short tendon.

Ptychadeninae

Ptychadena mascareniensis hylaea. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip, thin and approximately triangular, is wider at the origin and originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

Pyxicephalinae

Aubria subsigillata (fig. 11b). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short, thick, and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior fan-shaped slip is flat and wider at the origin, and

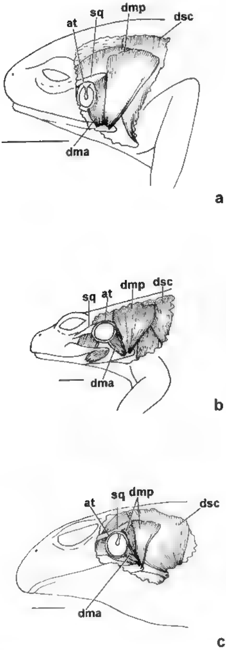


Fig. 11. – (a) *Cardioglossa cyaneospila* (FML 06477). Morphology corresponding to group XV (tab. 1). Scale bar: 0.5 mm. – (b) *Aubria subsigillata* (FML 03154). Morphology corresponding to group XIIb (tab. 1). Scale bar: 0.5 mm. – (c) *Rana angolensis* (FML 03188). Morphology corresponding to group Va (tab. 1). Scale bar: 0.5 mm. – Abbreviations: at, *anulus tympanicus*; dma, m. *depressor mandibulae anterior*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

originates on the dorsal fascia. It partially covers the m. *dorsalis scapulae* and m. *latissimus dorsi*. Both branches insert on the articular process of the lower jaw.

Raninae

Rana albolabris. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately triangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia covering the m. *dorsalis scapulae*. Both branches insert on the articular process of the lower jaw.

Rana angolensis (fig. 11c). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is a fan-shaped slip, wider at the origin and partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

Rana lepus. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the inferior edge of the *anulus tympanicus*. It is short thick and approximately rectangular. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*) and is fan-shaped and wider at the origin, with the fibers partially divided. Both branches insert on the articular process of the lower jaw.

FAMILY PETROPEDETIDAE

Phrynobatrachus acutirostris (fig. 12a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is approximately triangular, flat, thin and wider at the origin. Both branches insert on the articular process of the lower jaw.

Phrynobatrachus calcaratus. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is approximately triangular, flat, thin and wider at the origin. A nerve V branch passes through its fibers at mid-level. Both branches insert on the articular process of the lower jaw.

FAMILY HYPEROLIIDAE

Hyperoliinae

Afrixalus orophilus (fig. 12b). – It has a *depressor mandibulae* muscle divided into two branches. The anterior slip, approximately rectangular and narrow, originates on the anteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *levator mandibulae posterioris longus*), and the posterior edge of the *anulus tympanicus*. It is approximately triangular and wider at the origin. Both slips partially surround the tympanum. Both branches insert on the articular process of the lower jaw by a short and thin tendon.

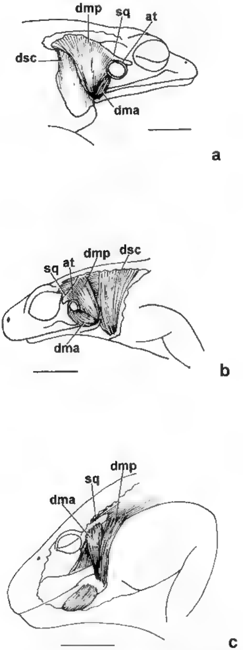


Fig. 12. – (a) *Phrynobatrachus acutirostris* (DIAM 006). Morphology corresponding to group Va (tab. 1). Scale bar 0.5 mm. (b) *Afrixalus orophilus* (FML 03229). Morphology corresponding to group XIV (tab. 1). Scale bar 0.3 mm. (c) *Rhinophrynus dorsalis* (FML 01720). Morphology corresponding to group IX (tab. 1). Scale bar 0.5 mm. – Abbreviations: at, *anulus tympanicus*; dma, m. *depressor mandibulae anterior*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

Chrysobatrachus cupreonitens. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is fan-shaped, wider and very thin at the origin, and thicker and narrower at the insertion point. The posterior slip partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

Kassininae

Kassina senegalensis angeli. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular and short, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is triangular, wider at the origin with a nerve V branch passing through it. This slip partially covers the anterior slip. Both branches insert on the articular process of the lower jaw by a short tendon.

Leptopelinae

Leptopelis notatus. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short, bulky and approximately fusiform, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is triangular, very wide at the origin and partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

FAMILY RHINOPHRYNIDAE

Rhinophrynus dorsalis (fig. 12c). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular and elongated, originates on the otic process of the squamosal. The posterior slip, very narrow, thin, and curved, originates on the dorsal fascia (at the level of the middle part of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

DISCUSSION

There is a considerable variation in the morphology of the m. *depressor mandibulae*. Nevertheless, fifteen morphological groups can be distinguished within the anuran species analysed (tab. 1). Although many studies have shown that the variation of the jaw muscles involves either their origin or insertion (ECKER, 1889, BEDDARD, 1908, 1911, EDGEWORTH, 1935, BALDAUF, 1955), in these fifteen groups, the insertion points of the m. *depressor mandibulae* is relatively invariant (see BAUER, 1997). The area of the origin on the posterior region of the head is also stable (allowing the muscle to open the mouth), except in *Hemisus*, *Arthroleptis* and *Breviceps* which have an extra anterior branch coming from the maxilla. Most variation involves muscle shape and often demonstrates intra- or intergeneric variation.

We found the following variation in the taxa analysed.

Table 1. Schematic representation of the different conditions of the *depressor mandibulae* muscle in anurans, with notation following Starrett (1968) and modifications in this work. Each group is identified by a Roman number (I to XV). Different morphotypes in a same group are identified by a letter (a, b, c or d). Superficial and deep slips of the *depressor mandibulae* muscle, when present, are identified by a subindex (1 and 2, respectively)

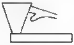
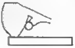
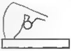
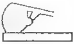
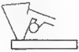
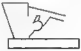
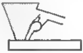
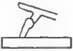
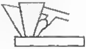
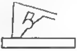
Group	Scheme		Taxa	Starrett, 1968	Present work
I			*Xenopus* *Alytes*	Dfsq DFa	Dfa DFa
II		**a**	*Chacophrys*	DFSQAT	DFSQ
		**b**	*Bufo arenarum*; *B. paracnemis*; *B. spinulosus* *Rhinophrynus*; *Melanophryniscus*	—— SQ	SQ SQ
		**c**	*B. g. major*; *Lepidobatrachus*; *Crinia* *Ceratophrys* *Hymenochirus*	—— DFSQAT SQ	Sqat SQat SQat
III			*Leptodactylus bufonius*; *L. chaquensis*, *Physalaemus biligonigerus*; *Crossodactylus*; *Taudactylus*	——	DFsq
IV			Pseudidae; *Scinax* *Gastrotheca* *Hyla andina*	—— *DFsq* DF	Dfsqat *DFsqat* Dfsqat
V		**a1**			
		**a2**	*Limnodynastes fletcheri*, *L. dorsalis*; *L. ornatus*; *Phrynobatrachus*; *Rana angolensis*; *Uperoleia borealis*	——	DFSQ-at_d
		**b1**			
		**b2**	*Dendrobates*	DFSQ$_d$at	DF-DF-sqat_d

Table I. – (Continuation)

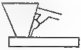
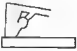
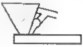
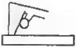
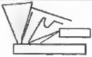
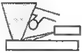
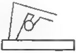
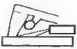
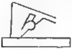
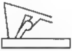
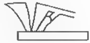
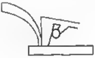
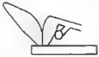
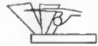
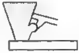
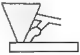
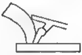
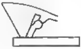
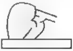
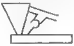
Group	Scheme		Taxa	STARRETT, 1968	Present work
V (cont.)		**c1**			
		**c2**	*Colostethus*; *Limnodynastes dumerili* *Pseudopaludicola boliviana*	----- DFSQ$_d$AT	DF-sqat$_d$ DF-sqat$_d$
		**d1**			
		**d2**	*Epipedobates*	-----	DF-at-sq$_d$
VI		**a**	*Hemisus g. guineensis*	-----	DF-sq-mx
		**b1**			
		**b2**	*Arthroleptis tuberosus*; *A. s. stenodactylus*	-----	DF-sq$_d$-mx
		**c**	*Breviceps*	-----	sq-mx
VII		**a**	Centrolenidae *Rhinoderma*	Dfa SQ	Sqat Sqat
		**b**	*Agalychnis*	-----	SQ-at
VIII			*Phyllomedusa* *Argenteohyla*	SQ -----	DF-SQ-at DF-SQ-at
IX			*Acris*, *Notaden*; *Ptychohyla*; *Smilisca* *Rhinophrynus*	----- SQ	df-SQ df-SQ

Table 1. – (Continuation)

Group	Scheme		Taxa	STARRETT, 1968	Present work
X			*Hyla boans*; *Pleurodema borelli*, Telmatobiinae	-----	DF-sq
			Plectrohyla	DF	DF-sq
XI			*Phrynohyas*	-----	DF-DF-at
XII		a	*Elachistocleis*, *Hoplobatrachus*	-----	DFat
		b	*Aubria*; *Chrysobatrachus*; *Conraua*; *Dermatonotus*; *Leptopelis*; *Phrynobatrachus*; *Phrynomantis*; *Ptychadena*; *Rana albolabris*; *R. lepus*; *Schoutedenella*	-----	DF-at1
			Kassina	DF AT	DF-at1
		c	*Limnodynastes convexiusculus*	-----	DF-at2
XIII			*Uperoleia aspera*	-----	DFSQat
XIV			*Afrixalus orophilus*	-----	DFsq-at
XV			*Cardioglossa*	-----	DF-sqat

Pipids and discoglossids have a single m. *depressor mandibulae*. STARRETT (1968) found that the apparent single muscle in *Xenopus* is a tripartite muscle, not very differentiated, but with three different origins (*anulus tympanicus*, dorsal fascia and squamosal). The only origin of the muscle on the dorsal fascia in our observations, with no apparent divisions, lead us to consider the m. *depressor mandibulae* morphology in *Xenopus* as a single one. Our descriptions of the *Alytes* m. *depressor mandibulae* agree with STARRETT's. However, in her descriptions, *Alytes* and *Xenopus* have different morphological patterns. In our case both taxa belong to the same group I.

Interestingly, both of these groups traditionally considered basal related to the Neobatrachia (FORD & CANNATELLA, 1993, CANNATELLA, 1999, MAGLIA et al., 2001; HAAS, 2001) have a simple morphology of the m. *depressor mandibulae*, with an origin on the dorsal fascia GRIFFITHS (1954) considered this state the primitive morphology of the muscle; but STARRETT (1968) did not agree with his hypothesis. *Hymenochirus* has a bulky m. *depressor mandibulae* like bufonids. This morphology was observed by STARRETT (1968) in some isolated species of different families. This situation is described by her also in *Rhinophrynus*. We could not find any fibers arising from the crista parotica in *Rhinophrynus dorsalis* as STARRETT (1968) described; we observed that all the muscle origins are at the otic ramus of the squamosal.

The Bufonidae analysed have a single bulky muscle similar to *Lepidobatrachus llanensis*, *Ceratophrys cranwelli* and *Chacophrys pierotti* (Leptodactylidae, Ceratophryinae) (group II, tab. 1). Ceratophryines have been considered alternatively related to bufonids (LIMESES, 1965), as a subfamily of the Leptodactylidae (Ceratophryinae) (LYNCH, 1973; HEYER, 1975; DUELLMAN & TRUEB, 1985) or a separate family (REIG, 1972). The particular morphology of the *depressor mandibulae* muscle in the Bufonidae (also considered by STARRETT, 1968, as a single slip with a non-fascial origin), seems to be a conservative condition and could be considered a primary homology shared by the Ceratophryinae-Bufonidae groups.

We found three more morphological patterns (groups III, V and X) for the rest of leptodactylids analysed. Only the species included in our group III have the pattern considered by STARRETT (1968) as the common type of the family, which includes origin from the squamosal. However, the inclusion of *Crossodactylus* in this group is at odds with her results. PALAVECINO (2000), analysing four of our species (*Physalaemus biligonigerus*, *Leptodactylus chaquensis*, *L. bufonius* and *Pleurodema borellii*), found very different patterns. All the species, except *P borellii*, are in our group III. The most striking difference is that in her results the m. *depressor mandibulae* origin never includes the squamosal (as it is in STARRETT, 1968, and in our results) This difference is probably related with the age (stage) of the specimens analysed. Another difference involves the *anulus tympanicus* that in our results in no case has any m *depressor mandibulae* fiber attached.

HEYER (1975) found six character states of the m. *depressor mandibulae* morphology in the leptodactylid frogs he analysed Among the genera analysed here, ten were also observed by him. Some of his results are coincident with ours. *Crossodactylus*, *Leptodactylus* and *Physalaemus* share the same pattern, described as B by HEYER (1975), and are together in our group III. In the other cases there are no coincidences at all.

Among hylids, we found seven different m *depressor mandibulae* morphologies (tab. 1) Within the genus *Phyllomedusa* we considered only those species with grasping feet All these species have the same morphological type of the *depressor mandibulae* muscle with three branches ("*partes*: *pars tympanica*, *pars squamosal* and *pars scapularis*") (group VIII, tab.1), similar to *Phyllomedusa atelopoides* (MANZANO, 1997), *P perinesos* (DUELLMAN, 1973), *P tomopterna* and *P tarsius* (CANNATELLA, 1980) The *Phyllomedusa buckleyi* group lacks the posterior branch of the *depressor mandibulae* muscle ("*pars scapularis*") as does *Agalychnis* (CANNATELLA, 1980) This particular condition was previously mentioned as one of the synapomorphies of the *buckleyi* group, suggesting that the genus *Phyllomedusa* is an unnatural assemblage of species (CANNATELLA, 1980) Moreover, some authors considered that the *buckleyi* group should be accorded generic status (DUELLMAN, 1968, 1969), representing a separate group closer to *Agalychnis* than to *Phyllomedusa*. All the species of this genus analysed by Starrett (1968), including *P. boliviana*, have the condition SQ. We found that *P. boliviana* and the other two species of this genus have the condition DF-SQ-at. The morphology of the m. *depressor mandibulae* in *Agalychnis saltator* (group VIIb) is similar to that of centrolenids described here (group VIIa), a condition also observed by Rueda-Almonacid (1994) in *Centrolene geckoideum*. However, there is a big variation within the Centrolenidae, exhibiting a *depressor mandibulae* muscle composed of two or three branches and different designs (Manzano, 2000), so the character is of limited usefulness in the comparison of both groups. Starrett (1968) considered a single slip lying over the squamosal as the pattern of adult centrolenids, but her results disagree with Manzano (2000) and ours.

Within the Hylinae, a large morphological diversity makes it impossible to assign them a single defined pattern. For example, *Acris crepitans*, *Ptychohyla ignicolor* and *Smilisca sila* have a morphotype similar to that of *Notaden* (a Myobatrachidae) and *Rhinophrynus dorsalis* (a Rhinophrynidae) (group IX, tab. 1). Our results disagree with Starrett's (1968). She found that *Acris* and *Ptychohyla* have a DF condition instead of df-SQ as in our specimens. In her results *Smilisca* has the condition DFsq, instead of df-SQ as in ours. *Hyla andina* and *Scinax fuscovarius* have a morphotype similar to that found in the Pseudidae and *Gastrotheca* (a Hemiphractinae hylid) (group IV, tab. 1). In our results, *Gastrotheca* has the condition DFsqat. Starrett (1968) found that the only hylid presenting an origin including the *anulus tympanicus* is *Cryptobatrachus fuhrmanni*. The morphology of the *depressor mandibulae* muscle in *Hyla boans* and *Plectrohyla guatemalensis* is similar to the Telmatobinae (Leptodactylidae) analysed and *Pleurodema borellii* (another leptodactylid) (group X, tab. 1). *Argenteohyla siemersi* has a morphology similar to that of the *Phyllomedusa* species analysed (group VIII). *Phrynohyas venulosa* has a morphology that differs from other groups and also from the rest of the hylids (group XI). Adding to this, Starrett (1968) found individual variation for the m. *depressor mandibulae* morphology in a series of *Hyla crucifer* from the same locality. No intraspecific variation was found in *Hyla* in this study.

The pseudids analysed (group IV, tab. 1) have a very characteristic morphological pattern of the m. *depressor mandibulae*, that is also present in *Scinax fuscovarius*, *Gastrotheca* and *Hyla andina*. This group includes species with the condition DFsqat. Starrett (1968) found the condition DFa for *Pseudis paradoxa*, again at odds with our results. It is interesting that Da Silva (1999) hypothesized in his phylogenetic analysis a relationship between Pseudidae and Hylinae.

Another example of intrageneric variation is found in the family Myobatrachidae. Within this family, *Limnodynastes fletcheri*, *L. dorsalis* and *L. ornatus* (Limnodynastinae) and *Uperoleia borealis* (Myobatrachinae) have similar morphologies (group Va, tab. 1) that differ from the rest of the myobatrachids previously analysed (*Limnodynastes convexiusculus*, group XIIc, *Crinia georgiana*, group IIc, and *Taudactylus diurnus*, group III). *Uperoleia aspera*, group XIV (Myobatrachinae) also presents a distinctive morphotype, not shared by other myobatrachids (groups Va and Vc, tab. 1). *Notaden* (Limnodynastinae) (group IX) does not share the myobatrachid morphology of the *depressor mandibulae* muscle.

Starrett (1968) described a *depressor mandibulae* muscle represented by three branches for the Dendrobatidae: two superficial, originating on the dorsal fascia and the *anulus tympanicus*, and a deep branch originating on the squamosal (based on *Epipedobates pictus*).

The condition that we observed in *Colostethus subpunctatus* (group Vc, tab. 1) was also described by Myers et al. (1991) for *Aromobates* and by La Marca (1995) for *Mannophryne*. In this case, the m. *depressor mandibulae* has two branches. Thus, there are at least two character states for the family with variation in the superficial branch. The particular disposition of the branches in relation to associated skull elements is common to most dendrobatids, which is why we insist on the existence of a characteristic morphotype for the family (groups Vb, Vc and Vd, tab. 1). In fact, Myers & Ford (1986), Ford (1989) and Ford & Cannatella (1993) considered the arrangement of the superficial slip of the m. *depressor mandibulae* as a synapomorphy of the Dendrobatidae.

The condition of the *depressor mandibulae* muscle in *Dermatonotus* and *Elachistocleis*, group XII (Microhylinae) is similar to that described by Burton (1983*b*) for other microhylids. Three origin points of the muscle are present in all microhylids analysed by him, except for the *Albericus* and *Choerophryne* data of Burton. *Breviceps poweri* (group VIc) has a morphology of the m. *depressor mandibulae* shared by *Arthroleptis* (group VIb) and *Hemisus* (group VIa). The morphotype of Microhylinae and Phrynomerinae *depressor mandibulae* is shared by some Ranidae (group XIIb), also mentioned by Hoyos (1999), including a nerve V branch that runs through the superficial slip of the muscle in most of the microhylids. This branch is also present in a leptodactylid, *Pseudopaludicola boliviana* (group Vc) and in an arthroleptid, *Cardioglossa* (group XV). Starrett (1968) considered the pattern for the species of ranids as DFAT and DFSQAT. We define also two morphotypes: DFat and DF-at, but neither of them includes a squamosal origin. Hoyos (1999) found a third branch arising from the squamosal. Although we could not find this branch, we agree with him with respect to sampling matters since we did not analyse all the same species.

The variation in our analysis far exceeds that described by Starrett (1968). In fact, we found only weak coincidences among her and our patterns (bufonids and some leptodactylids).

This leads us to believe that despite the great number of specimens analysed by various authors (Gaupp, 1896, Bigalke, 1926; Reig & Limeses, 1963; Limeses, 1965, 1969; Starrett, 1968; McDiarmid, 1971, Heyer, 1975; Emerson, 1976, Cannatella, 1980; Tyler & Davies, 1980; Davies & Burton, 1982; Burton, 1983*a*, *b*; Lynch, 1986, 1993, Cannatella & Trueb, 1988; Myers et al., 1991, Wake, 1993, Rueda-Almonacid, 1994, Burton & Zweifel, 1995, La Marca, 1995, Manzano, 1997, 2000, Hoyos, 1999), examination of additional specimens will doubtless uncover additional variation. Our frequent disagreement with Starrett (1968), Heyer (1975), Hoyos (1999) or Palavecino (2000) constitutes the rule rather than the exception. We think that this situation expresses the true characteristic of this muscle: its extreme variability. We agree with Lynch's (1973) conclusion that this muscle is of little use to analyse the relationships of eleutherodactyline frogs, and further extend his conclusion to the majority of the taxa observed by us.

The great diversity of the m. *depressor mandibulae* correlates with the plethora of patterns mentioned by Trueb (1993) for cranial morphology in Anura.

We find no evidence that variations in the m. *depressor mandibulae* are associated with particular habits. For example, *Hemisus g. guineensis* (group VIa, tab. 1) has a distinct morphology of the *depressor mandibulae*, formed by three well-differentiated slips with a particular anterior branch originating on the alary process of the maxilla by a tendon. This morphology can be interpreted as a muscle modification in relation to the animal's excavating habits, and the variation in the origin of this branch can be explained according to WAKE's (1993) interpretations. However, the presence of a similar morphotype in *Arthroleptis*, a non-excavating anuran, would falsify the hypothesis that intends to explain these morphologies as a function of a particular habit.

Nevertheless, there is a structural base of the muscle determined by its function as a mouth-opener. As the m *depressor mandibulae* opens the mouth, it must originate and insert in areas where this function is possible. The variations in the muscle shape, possibly determined by epigenetic factors, would be related to the switch from aquatic to terrestrial life habits. The remarkable consistency of this muscle in saurians and ophidians (Moro & Abdala, personal communication) allows us an epigenetic interpretation for the anatomic variability in anurans. However, the epigenetic action has constraints. For example: *Gastrotheca gracilis*, *G. chrysosticta* and *G. christiani* have different developments, direct and with tadpole larvae, needing very different environments to develop. However, and despite of variable epigenetic pressures on the different species mentioned, the m. *depressor mandibulae* morphology is exactly the same in all of them. Changes during early development of the jaw muscles with little or no effect on the adult morphology have been described previously for direct developing frogs (*Eleutherodactylus coqui*, by HANKEN et al., 1997).

Likewise, the presence of the same *depressor mandibulae* muscle structure in anurans with different diets (STARRETT, 1968) does not agree with EMERSON's (1985) idea about m. *depressor mandibulae* shape being directly related to feeding habits, which limits its action as an epigenetic factor

CONCLUSIONS

The morphology of the m. *depressor mandibulae* is too variable to be of much use in determining relationships or indicating habitat specializations. This variability seems to represent the most remarkable characteristic of this muscle.

In spite of the extreme variability of this muscle, we recognize some morphotypes that are useful to characterize some groups. They allow the use of the m. *depressor mandibulae* pattern as one character to be used in phylogenetic hypotheses including those groups.

ACKNOWLEDGEMENTS

We are grateful to Ronald Heyer, Tom Burton, Marissa Fabrezi and Greg Ellis for reviewing the manuscript and the language. Marvalee Wake made valuable comments. Raymond Laurent allowed us to use his African collection and M. J. Tyler generously made some specimens available. Thanks to J. Calvo for his assistance with the table. This work was partially supported by CONICET

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APPENDIX 1

MATERIAL ANALYSED

FAMILY DISCOGLOSSIDAE
    Alytes obstetricans (1). – FML 02782.

FAMILY PIPIDAE
  Dactylethrinae
    Xenopus laevis (2). – FML 03162.
    Hymenochirus boettgeri camerunensis (1). – FML 03113.

FAMILY BUFONIDAE
    Bufo arenarum (7). – FML 00540, 04722.
    Bufo granulosus major (5). – FML 01052, 04224.
    Bufo paracnemis (2). – FML 02168, 00364.
    Bufo spinulosus (4). – FML 00759.
    Melanophryniscus rubriventris rubriventris (8). – FML 02502, 02116.

FAMILY LEPTODACTYLIDAE
  Ceratophryinae
    Ceratophrys cranwelli (3). – FML 0492.
    Chacophrys pierottii (2). – FML 01020.
    Lepidobatrachus llanensis (3). – FML 01095, 05290, 08902.
  Hylodinae
    Crossodactylus gaudichaudii (1). – FML 03497.
  Leptodactylinae
    Leptodactylus bufonius (5). – FML 04642, 05364.
    Leptodactylus chaquensis (4). – FML 05490, 05111.
    Physalaemus biligonigerus (10). – FML 05288, 05986.
    Pleurodema borellii (6). – FML 01377, 02694.
    Pseudopaludicola boliviana (7). – FML 04307, 04309.
  Telmatobiinae
    Alsodes sp. (2). – FML 04435.
    Batrachyla sp. (1). – FML 03713.
    Hylorina sylvatica (1). – FML 03910.
    Telmatobius laticeps (3). – FML 03960.
    Telmatobius oxycephalus (3). – FML 02529.
    Telmatobius scrocchii (3). – FML 05772.

FAMILY MYOBATRACHIDAE
  Myobatrachinae
    Crinia georgiana (1). – DIAM 015.
    Taudactylus diurnus (1). – FML 03774.
    Uperoleia aspera (1). – DIAM 017.
    Uperoleia borealis (1). – DIAM 016.
  Limnodynastinae
    Limnodynastes dumerili (1). – DIAM 011.
    Limnodynastes convexiusculus (1). – DIAM 012.

Limnodynastes dorsalis (1). – DIAM 008
Limnodynastes fletcheri (1). – DIAM 009
Limnodynastes ornatus (1) – DIAM 010
Notaden melanoscaphus (16). – FML 03783, DIAM 013.
Notaden nichollsi (1). – DIAM 014.

FAMILY RHINODERMATIDAE
Rhinoderma darwinii (4) – FML 03694

FAMILY HYLIDAE
Hemiphractinae
Gastrotheca gracilis (6). – FML 01769, 02209.
Gastrotheca christiani (2 adults and 3 juveniles) – FML 02117, 02918
Gastrotheca chrysosticta (2). – FML 02759.
Hylinae
Acris crepitans (1). – FML 09478.
Argenteohyla siemersi (4). – FML 00056
Hyla andina (3). – FML 04758, 00698
Hyla boans (1). – RL 105039, FML 09543.
Phrynohyas venulosa (3). – FML 02303, 02712.
Plectrohyla guatemalensis (1). – RL 64105.
Ptychohyla ignicolor (1) – RL 137222
Scinax fuscovarius (4). – FML 04635, 02716, 02754
Smilisca sila (1) – RL 918887
Phyllomedusinae
Agalychnis saltator (1). – FML 09541.
Phyllomedusa boliviana (4). – FML 01345, 02706.
Phyllomedusa hypocondrialis (4). – FML 01483, 04286
Phyllomedusa sauvagii (4). – FML 04899

FAMILY CENTROLENIDAE
Centrolene grandisonae (1). – FML 04980.
Cochranella ignota (3). – FML 04965, UVC 12091.

FAMILY PSEUDIDAE
Lysapsus limellus (3). FML 04341, 00791.
Pseudis minutus (3) – FML 03676.
Pseudis paradoxus (6). – FML 00708, 04661, 00936.

FAMILY MICROHYLIDAE
Brevicipitinae
Breviceps poweri (1). – FML 03165
Microhylinae
Dermatonotus muelleri (5). – FML 05365, 01074.
Elachistocleis bicolor (7). – FML 00251, 00151, DIAM 029
Phrynomerinae
Phrynomantis bifasciatus (1). – FML 03029

FAMILY DENDROBATIDAE
Colostethus subpunctatus (1). – FML 02598
Dendrobates auratus (1) FML 01722.
Epipedobates pictus (1). FML 03516

FAMILY HEMISOTIDAE
Hemisus guineensis guineensis (3). – FML 01244

FAMILY ARTHROLEPTIDAE
- Arthroleptinae
  - *Arthroleptis stenodactylus stenodactylus* (1). – FML 00066.
  - *Arthroleptis tuberosus* (2). – FML 00051.
  - *Cardioglossa cyaneospila* (1) – FML 06477.
  - *Schoutedenella* sp. (1). – RL Lote 24.
  - *Schoutedenella sylvatica* (1). – RL Lote 231.

FAMILY RANIDAE
- Dicroglossinae
  - *Conraua crassipes* (2). – FML 03068.
  - *Hoplobatrachus occipitalis* (1). – No data
- Ptychadeninae
  - *Ptychadena mascareniensis hylaea* (3). – FML 01228.
- Pyxicephalinae
  - *Aubria subsigillata* (1). — FML 03154
- Raninae
  - *Rana albolabris* (2). – Lote 231.
  - *Rana angolensis* (3). – FML 03188.
  - *Rana lepus* (1). – RL Lote 231.

FAMILY PETROPEDETIDAE
- *Phrynobatrachus calcaratus* (2). – RL Lote 231
- *Phrynobatrachus acutirostris* (1) – DIAM 006.

FAMILY HYPEROLIIDAE
- Hyperoliinae
  - *Afrixalus orophilus* (4). FML 03229, 03230.
  - *Chrysobatrachus cupreonitens* (3). – FML 02081.
- Kassininae
  - *Kassina senegalensis angeli* (2). – FML 02076.
- Leptopelinae
  - *Leptopelis notatus* (2). – FML 03205

FAMILY RHINOPHRYNIDAE
- *Rhinophrynus dorsalis* (1). – FML 01720.

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